

SOUND PRODUCTION IN THE SNAPPING SHRIMPS *ALPHEUS* (*CRANGON*) AND *SYNALPHEUS*^{1,2}

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Many marine organisms are sources of sound in the sea, especially fishes and mammals. Among the invertebrates, the Crustacea include the most prodigious sound producers, for example, the spiny lobsters (Palinuridae) (Dijkgraaf, 1955; Moulton, 1957; Hazlett and Winn, 1962), stomatopods, and some crabs. But the sounds of these are not so persistent and widespread as the noise produced by snapping or pistol shrimps of the genera *Alpheus* (*Crangon*) and *Synalpheus*, which inhabit warmer seas.

Although it has long been known that a snapping shrimp is capable of emitting a loud "snap", the "crackling" noise produced by vast numbers of these shrimps was formerly attributed to a variety of things, *e.g.*, water noise, *Teredo* boring on ship hulls, terrestrial disturbances, and many other phenomena. Hulburt (1943) speaks of a crackling noise similar to that produced by "dragging a blackberry bush" which he heard at various places along the southern coast of the United States.

Early in 1942 a similar crackling noise of unknown origin was heard in various localities off the coast of California. F. A. Everest, R. H. Fleming, M. W. Johnson, and R. W. Young, of the University of California's Division of War Research, determined that the sound was due to a continuous fusillade of snaps from millions of snapping shrimps (Johnson, 1943; Everest, Young and Johnson, 1948).

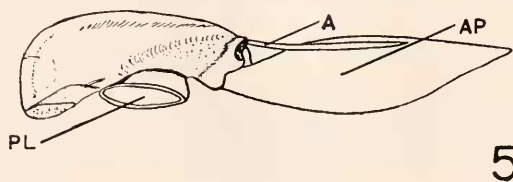
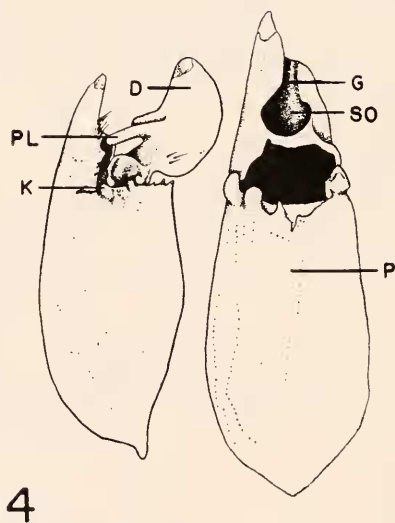
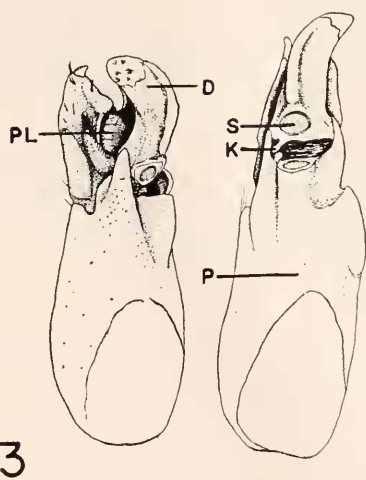
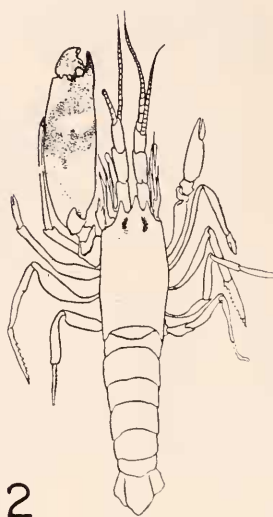
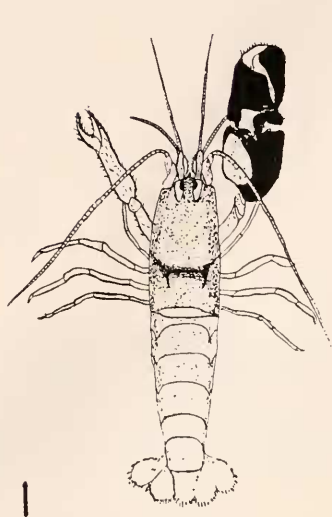
Snapping shrimp sounds have been analyzed by several investigators (Loye and Proudfoot, 1946; Johnson *et al.*, 1947; Everest *et al.*, 1948; Johnson, 1948; Knudsen *et al.*, 1948; Dobrin, 1949; Shishkova, 1958). The present paper deals primarily with the characteristics of snapping shrimp sounds of Bermuda waters, and examines further the derivation of ecological data from the analysis of underwater sounds. The anatomy and physiology of the sound-producing organ are also discussed.

The sounds analyzed in this study were recorded at Bermuda from June to August, 1958. The recording equipment consisted of an AX-58-C Rochelle salt hydrophone, a Woods Hole suitcase amplifier, and an Ekotape tape recorder model 205 or a PT6-BN and a PT6BA2HZ Magne recorder tape recorder. Recordings were made so that the nature of the sounds could be determined for different

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FIGURES 1-5.

depths and bottom conditions. Single snaps recorded in the laboratory were also studied. The recordings obtained were analyzed on a Kay Vibralyzer vibration frequency analyzer.

STRUCTURE OF THE SOUND-PRODUCING CHELA

The first pereopods of the members of the Family Alpheidae, to which the snapping shrimps belong, bear dissimilarly enlarged chelae. The larger claw, a weapon of offense and defense, produces the snapping sound. Its anatomy, from the point of view of sound production, has been partially elucidated (Volz, 1938; Johnson *et al.*, 1947; Hazlett and Winn, 1962). MacGinitie (1937) observed this claw's use as a weapon of food capture (see MacGinitie and MacGinitie, 1949, pp. 276-279, for further discussion of the animal's habits.) The smaller claw is used mainly in grasping and handling objects. In *Alpheus heterochelis* and *A. normanni*, of North Carolina, approximately half of a chance collection will be "right-handed" (the claw on the right will be the larger one in a dorsal view, as in Figure 1) and the other half will be "left-handed." It has been shown for several species of *Alpheus* and *Synalpheus* that when the large chela or crusher is removed, a small chela or nipper is regenerated from the stump of the larger one, the original nipper differentiating into a crusher at the next molt. This "chela reversal" was first noted by Przibram (1901), and several hypotheses have been advanced in explanation (Wilson, 1903; Darby, 1934; Dawes, 1934). Chela reversal is doubtless of biological advantage to the animal, for it permits more rapid formation of the crushing claw than would otherwise be the case.

It is of interest to note that the dactylopodite or "movable finger" of the *Alpheus* and *Synalpheus* snapping chela lies laterally on the propodite or "hand," in contrast to other typical decapods, in which it lies medially. This difference is due to a very flexible joint between the propodus and carpus. In many decapods this joint is hinge-like, and the dactylus is always held medially. In alpheids, on the other hand, flexibility of the joint allows the animal to rotate the propodite 180°, so that the dactylopodite can be held either laterad or mediad to the body. Although the dactylopodite is normally held laterad, turning over the propodite so that the dactylopodite is mediad causes no apparent injury or annoyance to the animal; however, we have not observed a shrimp snapping its chela in the inverted position.

The portions of the snapping chela that are most important in production of sound are the propodus and the dactylus. In both *Alpheus* and *Synalpheus* these portions of the large chela are proportionately enormous, but there are distinct anatomical differences between the two genera which have not hitherto been pointed

FIGURE 1. *Alpheus heterochelis*, dorsal view, $\times 2$. After Brooks (Brooks and Herrick, 1891).

FIGURE 2. *Synalpheus minus*, dorsal view, $\times 5$. Drawn from life.

FIGURE 3. Large chela of *Alpheus peasei*, lateral (left) and dorsal (right) views, $\times 6$. Drawn from life. D, dactylus; P, propodus; PL, plunger; S, oval disc; K, exoskeletal knob.

FIGURE 4. Large chela of *Synalpheus minus*, lateral (left) and dorsal (right) views, lateral view with dactylus removed to show water jet groove, $\times 15$. Drawn from life. D, dactylus; P, propodus; PL, plunger; SO, socket; K, exoskeletal knob; G, water jet groove.

FIGURE 5. Dactylus of large chela of *Alpheus californiensis* showing exoskeletal extensions, dorsal view, $\times 8$. Drawn from life. PL, plunger; A, apodeme; AP, apodemal plate.

out and which are reflected in respective acoustical spectra. The chela is generally ellipsoidal and more swollen in *Synalpheus* (Fig. 2) than in *Alpheus*, where it is somewhat compressed (Fig. 1). *Synalpheus* chelae are simple and have no notches or grooves, but those of *Alpheus* species are usually notched and deeply grooved (Fig. 3).

Another generic difference lies in the arrangement of the tips of the terminal articles. In species of *Synalpheus*, the chela tips are directly opposed, but in species of *Alpheus* we have studied, the closing surfaces are arranged somewhat like shears. The distal part of the dactylus closes on a chitinous projection from the propodus. Consequently, in *Alpheus* the sides of the chela tips come together.

Both *Alpheus* and *Synalpheus* possess a tooth-like "plunger" on the dactylus which fits into a "socket" or pit on the propodus when closed. The structure of the plunger and socket differs in the two genera. In *Synalpheus* the plunger is subdivided into a double rod (Fig. 4), while in *Alpheus* it is oval and single (Fig. 3). The socket in *Synalpheus* is narrow to accommodate the thin rod, but in *Alpheus* it is larger and deeper since the plunger is bigger and longer. There are other minor differences which reflect a greater degree of specialization in *Alpheus*.

THE SNAPPING MECHANISM

Even at present the exact mechanism by which the snap is produced is uncertain. An early hypothesis attributed the sound to a rubbing of the basal spines of the uropods (Lovett, 1886), and Miner (1950, p. 494) erroneously states that it is caused by a flicking of the wrist joint of the crusher claw. In the living animal, one can easily see that movement of the dactylus of the large claw immediately precedes the snap.

The first careful observations on the way in which the alpheid chela produces sound were made by Kent (1877), but he erroneously attributed it to a sudden opening of the dactylus. Herrick (Brooks and Herrick, 1891) was perhaps the first to correctly describe how the sound is produced. As he points out, the sound is caused by impact of the hardened claw tips coming together as the plunger of the dactylus is driven into the socket of the propodus. Anterior to the socket is a groove through which a jet of water escapes when the plunger suddenly clamps down on the socket (Fig. 4). The main function of the plunger-socket mechanism is not production of sound, but of this water jet, which stuns or frightens enemies. The sound which is produced simultaneously is a "by-product" of this protective movement (Schmitt, 1931, p. 192; Johnson *et al.*, 1947; Moulton, 1957).

Closure of the large chela works much like the uncocking of a pistol hammer. Mechanics of the cocking mechanism, however, are still in doubt. Courti re (1899), Verrill (1922), and Johnson *et al.* (1947) maintain that two oval discs or hardened surfaces (Fig. 3), which come in contact with each other when the dactylus is raised to its fullest extent, serve as "suckers." According to this view, when the dactylopodite is raised, these surfaces adhere to each other like two panes of damp glass. Extra tension must be built up by the adductor muscle in order to break the contact between the suckers, and this increases the impact force. These hardened discs probably do not serve this function, however. They are absent in species of *Synalpheus*, which are also capable of vigorous snapping, and

they are present in *Amphibetaeus* species, which are incapable of snapping. The suggestion by Johnson *et al.* (1947) that analogous smooth surfaces of *Synalpheus* serve the same purpose as the "suckers" of *Alpheus* we cannot verify, nor could we demonstrate any suction mechanism in preserved specimens of *A. californiensis*, which were studied by them, and *A. heterochelis*. We found that the dactylus could be moved freely in and out of the well, a fact observed also by Herrick (Brooks and Herrick, 1891). Further, it would be expected that if these discs were functional in producing suction, they would be membranous in character; they seem to be chitinous and no different from the rest of the exoskeleton. It is possible that in the living animal, when the dactylopodite is pulled up and comes in contact with the propodite, the membrane connecting the segments depresses. This depression may cause a partial suction to build up and hold the dactylus and propodus together until the muscular tension is sufficient to overcome the additional resistance.

In *Synalpheus* a type of cocking device depending on overlap of exoskeletal knobs may serve to hold the dactylopodite in place. In two species of *Synalpheus* (*S. minus* and *S. goodei*) there are white exoskeletal projections lying dorsad on the chela (Fig. 4). Matched protuberances on the propodus and dactylus slide over each other easily as the dactylus is opened, and they serve to hold it in the raised position against considerable tension. As contraction overcomes friction thus provided by the cocking device, the dactylus closes and a snap results. These disarticulating knobs are not equally evident in all species of *Alpheus*, although a similar mechanism may occur throughout the genus.

In addition to the investigators mentioned above, Dobrin (1949) and Moulton (1959) studied the mechanism producing the noise, but knowledge regarding the exact nature of the snapping mechanism still remains scanty, mostly because the many speculations have not been proved by experimentation.

ANATOMY AND PHYSIOLOGY OF THE CHELA MUSCULATURE

Both the abductor and adductor muscle fibers of the dactylus originate on the dorsal and ventral walls of the propodus. The abductor fibers have their insertions on an exoskeletal extension of the dactylus called the apodeme, which is attached to the outer basal angle of the dactylopodite. The muscle fibers of the adductor are more numerous and are inserted on both sides of a large, flat apodemal plate attached to the inner basal angle of the dactylus (Fig. 5).

Physiological studies on the large chela of *A. heterochelis* indicate that the characteristics and innervation of the claw muscles are probably no different from other Crustacea (see Prosser, 1950, pp. 595-614, for a discussion of crustacean muscle and innervation). Both fast and slow types of contraction were demonstrated when the adductor muscle of an isolated *A. heterochelis* claw was stimulated with electrical shocks from an electronic stimulator (Fig. 7). The fast twitch takes place in about 0.1 second, while the slow contraction lasts for more than a second and may be even longer, depending upon duration of the stimulus. This muscle is thus doubly excitable, *i.e.*, it exhibits two distinct types of response, depending upon intensity and frequency of the stimulus. The dactylus adductor is equivalent to two physiologically differentiated units. Separation into slow and

fast movements has decided functional significance. The slow system is used in normal movements of the dactylus. The fast system is brought into play when great tensions are needed to crush objects. That the muscle is innervated by separate fast and slow fibers (as in many other crustaceans) has not been demonstrated histologically. Indeed, a bifunctional single nerve fiber system may be present in snapping shrimp chela musculature. However, the double excitable system is more efficient and it exists in crustacean muscles which develop considerable power. In order to create rapid movements, it seems logical that a special fast fiber system would be advantageous in the muscle.

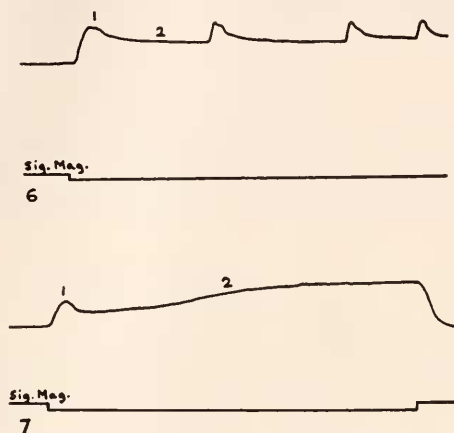


FIGURE 6. Tracing of kymograph record showing fast and slow contractions in adductor muscle of dactylus of *Alpheus heterochelis* large chela.

FIGURE 7. Tracing of kymograph record showing inhibitory effect in adductor muscle of dactylus of *Alpheus heterochelis* large chela.

When the adductor muscle of *A. heterochelis* was stimulated, fast contractions occasionally appeared superimposed on the slow contraction. This effect can be seen in Figure 6. It may be due to simultaneous excitations of both excitatory and inhibitory fibers. The initial contraction (represented by 1) is of the fast type. The tension developed is maintained by the slow contraction (represented by 2). But in this case there is very little summation in the slow contraction, unlike that shown in Figure 7. This may be due to inhibition of the slow contraction by stimulation of inhibitory fibers. The inhibitory effect is overcome when another fast contraction results from stimulation of an excitatory fiber, as shown by the next fast contraction. Possibly the re-emergence of the fast contraction may be due to an elimination of an inhibitory substance by an excitatory substance and the subsequent accumulation of the excitatory substance. A similar rhythmic response was recorded by F. P. Knowlton (1942) on crab claw muscle. These rhythmic contractions are believed to have been due to simultaneous stimulation of inhibitory fibers or nerve endings (F. P. Knowlton and Campbell, 1929).

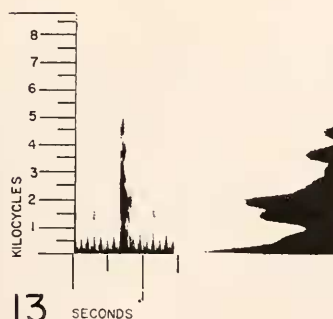
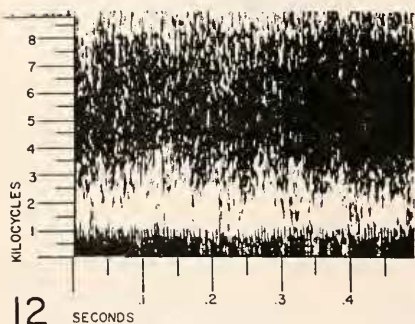
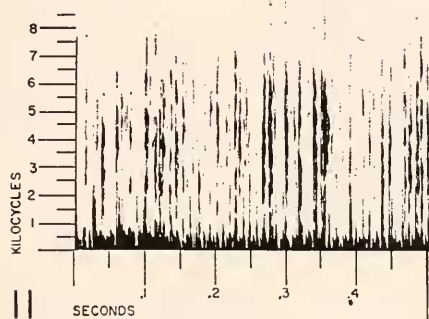
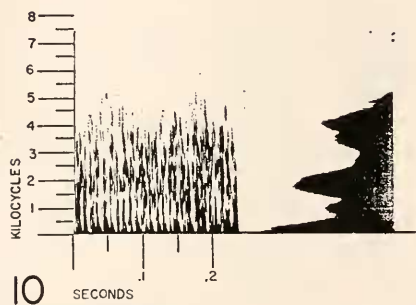
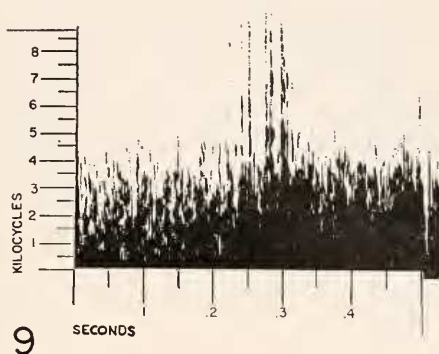
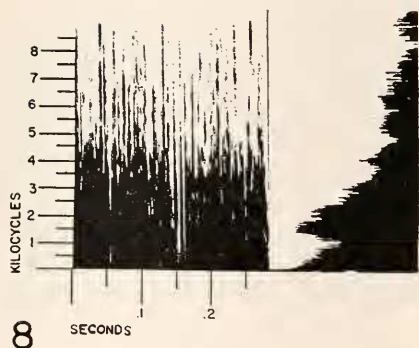


FIGURE 8. Vibrogram (left) and section (right) of snapping shrimp noise.

FIGURE 9. Vibrogram showing snapping shrimp "volleys."

FIGURE 10. Vibrogram and section of water noise.

FIGURE 11. Vibrogram of snapping shrimp noise with water noise at a minimum.

FIGURE 12. Vibrogram of snapping shrimp noise at Bimini, Bahama Islands.

FIGURE 13. Vibrogram and section of a single *Synalpheus minus* snap.

RECORDING AND ANALYSIS OF BERMUDA SNAPPING SHRIMP NOISE

Recordings were made at 56 stations surrounding the Bermuda, Challenger, and Argus (Plantagenant) Banks in the Western Atlantic Ocean. During the recordings the hydrophone just cleared the bottom. Sound waves picked up by the hydrophone were recorded on the tape recorder either at $7\frac{1}{2}$ or $3\frac{3}{4}$ inches per second. Snapping shrimp noise did not occur at all stations, but when it was present it remained fairly continuous throughout the recording. Other noises heard in conjunction with snapping shrimp noise include *Holocentrus ascensionis* (squirrelfish) volleys, *Epinephalus striatus* (Nassau grouper) grunts, *Panulirus argus* (spiny lobster) stridulations, and *Gonodactylus oerstedii* (mantis shrimp) raptorial sounds.

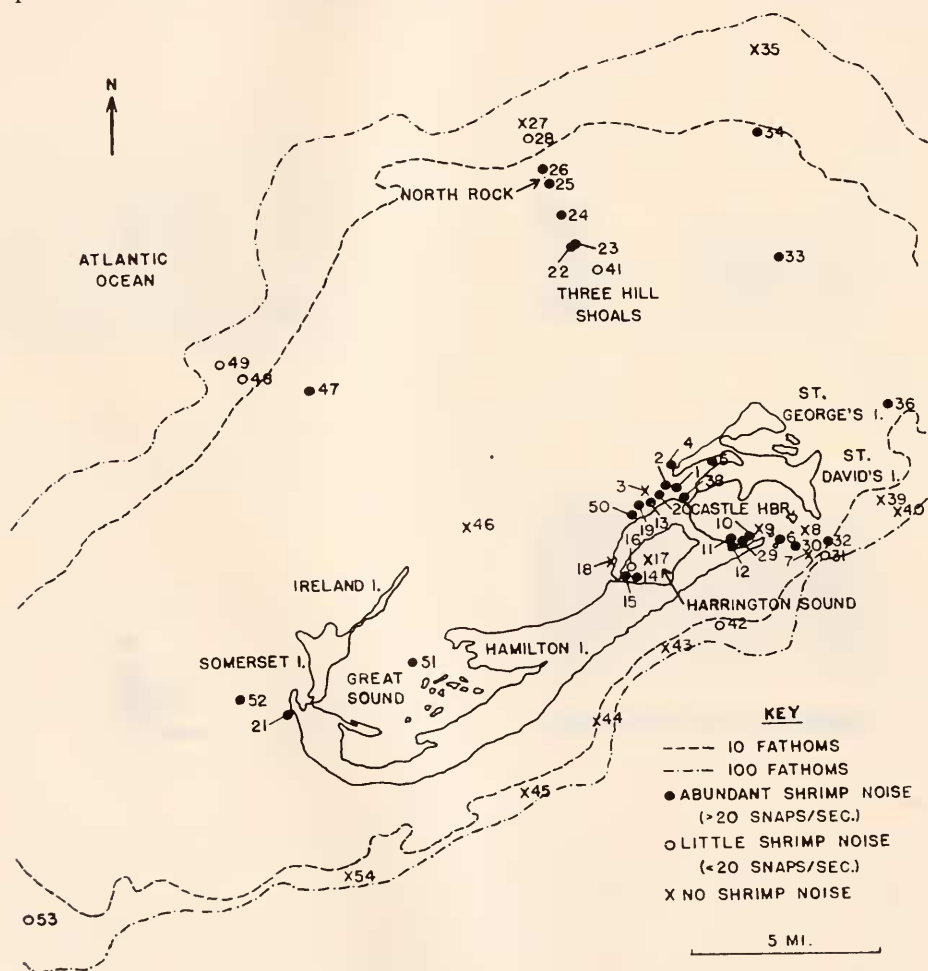


FIGURE 14. Map of Bermuda showing location of the 56 stations and the amount of noise heard at each station. Station 37 (Ariadne Bank), located to northeast, stations 55 and 56 (Challenger and Argus Banks), located to southwest off the map.

Figure 8 represents a typical spectrum of snapping shrimp noise, as analyzed by the Vibralyzer. To the left is a frequency-time portrayal known as a vibrogram, where time is plotted on the horizontal axis and frequency on the vertical axis. Each vertical "spike" (which is seen most clearly in the upper half of the vibrogram) represents a snap from an individual snapping shrimp. To the right of the vibrogram in Figure 8 is a section which reveals the relationship between intensity and frequency at a preselected point in time. A qualitative measure of relative intensity is portrayed on the horizontal axis in a linear scale and frequency on the vertical axis.

A random 1.2-second interval of shrimp noise from each station was recorded onto and analyzed by the Vibralyzer. The frequency range of every vibrogram and section made was 88–8800 cycles per second. In all vibrograms band-width is wide, shape flat, and pattern normal. One vibrogram and sections of two or three points in the vibrogram were made at each station.

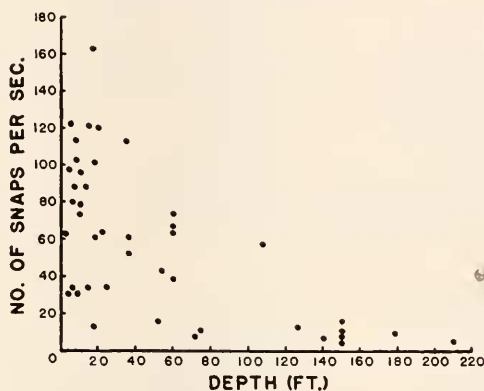


TABLE I

A description of the localities of snapping shrimp recordings at Bermuda during the summer of 1958, the number of snaps/second counted, and the frequencies of highest intensity, as well as relative intensity

Station number	Location	Depth (ft.)	Bottom conditions	No. of snaps per sec.	Pt. of highest intensity	
					Freq. (kc)	Rel. int.
1	Inside western entrance to Ferry Reach	8	Sandy, near submerged rock and sponge clump	103	3.0	4.5
2	Outside western entrance to Ferry Reach	20	Rocky	120	3.2	3.5
3	Directly in front of Ferry Reach	48	Level sand, some grass and low coral	—	4.3	2.7
4	Whalebone Bay	7	Large coral reef	88	3.2	4.3
5	Dock of Bermuda Biological Station	15	Wharf made from rock piling	121	4.5	3.8
6	Southeast of Castle Island	17	Rocky, some sand and grass	163	4.8	2.7
7	Southwest of Castle Roads	60	Sand, some rocks	—	1.8	3.8
8	Northeast of Gurnet Rock	20	Rocky	—	3.1	1.3
9	Castle Harbor over Great Shoal	2	Shoal	—	0.5	5.1
10	Mouth of Wallace Bay	6	Rock ledges	80	1.9	6.0
11	Little Harbor in Tuckerstown	25	Rock ledges	35	2.2	2.9
12	Mouth of narrow reach north of opening to Tuckerstown Bay	4	Rock ledges	31	3.5	2.1
13	Bailey's Bay between Bay Island and East Point	4	Rock and sand	97	3.5	3.8
14	Harrington Sound side of Flatts Bridge	35	Rocky with bottom growth	113	2.7	4.7
15	West of Flatts Inlet	5	Rock ledges	122	3.5	2.1
16	Green Bay of Harrington Sound	18	Rock ledges and deep cave	12	2.2	3.5
17	Harrington Sound straight out from Green Bay	55	Sand	—	1.0	2.9
18	East side of Shelly Bay	10	Shoal	—	0.8	5.0
19	East side of Bay Island	13	Rocky	88	2.1	4.7
20	West side of Bay Island	2	Rocky	63	2.0	5.3
21	South of Wreck Hill	8	Shallow coral reef	113	0.8	5.5
22	North reefs short of North Rock (recorded in early evening)	10	Shallow coral reef	96	1.7	5.6
23	North reefs short of North Rock (recorded during daytime)	10	Shallow coral reef	73	1.3	5.8
24	North reefs short of North Rock	18	Broken bottom	101	1.4	4.0
25	South of North Rock	10	Broken bottom	78	2.7	5.8
26	North of North Rock	18	Rock ledges	61	1.9	5.6
27	Northwest of North Rock	360	Edge of Bermuda Bank	—	0.0	5.3
28a	Northwest of North Rock	168	Edge of Bermuda Bank	9	1.9	5.4
28b	Northwest of North Rock	126	Edge of Bermuda Bank	12	0.2	6.2
28c	Northwest of North Rock	108	Edge of Bermuda Bank	57	1.7	4.9
28d	Northwest of North Rock	210	Edge of Bermuda Bank	4	1.9	4.9

TABLE I—(Continued)

Station number	Location	Depth (ft.)	Bottom conditions	No. of snaps per sec.	Pt. of highest intensity	
					Freq. (kc)	Rel. int.
28e	Northwest of North Rock	150	Edge of Bermuda Bank	15	0.8	4.0
29	Mouth of Wallace Bay	22	Just off rock ledges over sand	64	1.7	5.8
30	Castle Roads south of Charles Island and southwest of Gurnet Rock	54	Sand and sponges	43	1.9	5.2
31	Castle Roads southeast of Charles Island	150	Sand and scattered bottom growth, some rocks	7	0.4	5.5
32	Castle Roads southeast of Castle Island and south of Nonesuch Island	60	Rocky coral broken by level patches of sand	38	3.5	2.9
33	North of St. Catherine's Point	36	Coral reef	52	2.9	5.6
34	North of St. Catherine's Point	60	Rocky	67	3.0	4.8
35	North of St. Catherine's Point	150	Rock ledges	—	0.0	3.9
36	Northeast of St. George's Harbor	60	Rocky	63	1.0	5.7
37	Northeast of St. George's Harbor near Ariadne Bank	140	Rocky	6	1.8	5.2
38	Ferry Reach	9	Old anchored barge	30	4.3	3.2
39	Southwest of St. David's Island	70	Sand, scattered rocks	—	1.9	4.2
40	Southwest of St. David's Island	138	Sand, scattered rocks	—	2.4	3.1
41	North Reefs near Three Hill Shoals	54	Sunken wreck	15	3.8	4.9
42	South of Sam Hall's Bay	72	Rock ledges and sand	7	1.7	4.4
43	South of Town Hill	144	Sand	—	1.9	3.2
44	Southeast of Elbow Beach	60	Sand	—	2.3	2.6
45	White Cliffs toward Warwick Long Bay	138	Sand	—	0.5	4.7
46	Brackish Pond Flats vicinity in northwest harbor basin	45	Sand	—	2.0	2.8
47	Inside northwest reefs	6	Rock ledges	34	2.3	5.4
48	Outside northwest reefs	75	Sand and some rocks	11	0.9	5.2
49	Outside northwest reefs	150	Rock ledges	10	1.8	5.3
50	Bailey's Bay	15	Sand and some rocks	34	2.3	3.0
51	North of Pearl Island	36	Coral reef	61	1.5	4.8
52	West of Wreck Hill	60	Coral reef	73	1.7	4.5
53	Southeast of Wreck Hill	150	Rock ledges	3	0.7	5.8
54	South of Wreck Hill	84	Rock ledges and sand	—	0.8	5.2
55	Challenger Bank	168	Coral reef	—	0.8	3.6
56	Argus Bank	168	Coral reef	—	1.0	4.0

in Table I. Location of each of the 56 stations as well as the amount of noise heard at each station is shown in Figure 14.

DEPTH

Figure 15, in which relative abundance of snapping shrimp (measured by the number of snaps per second) at each of 46 places where shrimp noise was heard is plotted against the depth of each station, indicates depths most favorable and least

favorable to snapping shrimp populations. Above 120 feet there is a great deal of variation in the abundance of snapping shrimps. Except for six stations at less than 120 feet, shrimp crackle was very intense. At some of these stations it could be heard above the surface of the water by ear. The noise was most intense in Ferry Reach, near Castle Island, and near Flatts Bridge. At all stations where depth exceeded 120 feet, there was little shrimp noise (less than 20 snaps per second) or none at all.

Data from trawling and dredging collections indicate that most of the species occur in the 0–30 fathom range. Acoustical data corroborate this finding. Loye and Proudfoot (1946), Johnson *et al.* (1947), Everest *et al.* (1948), and Knudsen *et al.* (1948) have shown that sound levels are low in water deeper than 180 feet, even if bottom conditions are favorable. Knudsen *et al.* found that “highest noise levels appear to occur in water between 30 and 140 feet deep.” However, in Bermuda, shrimp crackle was most intense in the 0–120 feet range, particularly in depths less than 40 feet.

Shrimp noise gradually tapers off with increasing depth. Near North Rock (Stations 25 and 26) the level of shrimp noise was relatively high. In deeper water, about a thousand feet northwest of North Rock (Station 28), shrimp appeared to be less numerous (as indicated by fewer snaps per second). A little farther off the edge of Bermuda Bank (Station 27) at 360 feet, no snapping shrimp noise was heard. Deep-water forms do occur, but not in sufficient numbers to produce the crackling sound typical of shallow water. In general, if bottom conditions are favorable, the relative abundance of snapping shrimp varies inversely with depth.

BOTTOM CONDITIONS

Snapping shrimps occur mainly on substrates which afford shelter, such as rocks, coral, plant growth, or litter; only rarely on sand and mud bottoms. Many species live in association with other organisms. *Synalpheus* species are very numerous in large sponges (Coutière, 1910; Goode, 1878; Herrick, 1886; Hay and Shore, 1915–1916; Pearse, 1934, 1950). Snapping shrimps have been found living in burrows made by annelids or mollusks (Coutière, 1899), clinging to crinoids (Coutière, 1909), as commensals with tube worms (MacGinitie, 1935; Banner, 1953), anemones (Clarke, 1955), and ascidians (Lebour, 1938).

The Bermuda data indicate that snapping shrimps occur in great numbers only when sheltering materials are present. At almost every station where snapping shrimp noise was heard, the substrate consisted either of rock or coral. Conversely, at almost all stations with broken substrates (and less than 210 feet depth), snapping shrimp noise was heard. Apparent exceptions were Stations 7, 8, and 9, at the mouth of Castle Harbour. Much shrimp noise was heard at other stations in the area, and it would be expected that the noise would also have been heard at Stations 7, 8, and 9. Although no snaps were recorded, shrimp may have been present and their noise may have been cancelled by the great amount of water noise caused by the rough seas encountered at the time of recording. Stations with rocky coral bottoms had the highest level of shrimp noise.

In Bermuda the “sand” is not silicious but calcareous. In fact, at least 90% of all bottom deposits is composed of calcareous material (Bigelow, 1905). The

south shore of Bermuda abounds in fine calcareous sand. As is to be expected, no shrimp noises were recorded near the south shore (Stations 43–45 and 54). Similarly, Johnson *et al.* (1947) and Shishkova (1958) never heard shrimp noise in areas with a sandy bottom.

At the deep Challenger and Argus Bank stations, where single snaps were not very numerous, snaps that were recorded on the vibrograms frequently occurred in clusters (Fig. 9). Although no snaps were recorded during the random time interval, occasional "volleys" of shrimp noise were heard. These bursts of snaps probably originated from groups of shrimps hiding under occasional cobbles.

TEMPERATURE

Slight temperature changes do not appear to have any great effect on snapping shrimp activity, but prevailing temperature determines their distribution. Their numbers dwindle as the water becomes colder. Specimens kept in glass aquaria survive well as long as the water temperature remains between 14 and 24° C. They can stand high temperatures and salinities and long periods without food. One specimen lived for months without food in an aquarium where the temperature reached 27° C. and the salinity was 45‰ (A. B. Williams, personal communication). They are more sensitive to low temperature.

An interesting situation described by Boden (1952) occurs on the edge of the Bermuda Bank. A convection current system exists where warm water of the lagoon flows over the bank until it converges with the surface of the colder ocean water. As the warm water is cooled, it sinks and the current is set up. In this way most of the warm lagoon water is returned to the lagoon. Plankton is more abundant in the lagoon, but much of it spills over the bank by means of this current system. Because larval forms of most species of snapping shrimp are planktonic, it is possible that shrimp larvae may be carried over the bank. This may explain why some shrimp noise was heard at the stations near the bank (Stations 28, 48 and 49). Snapping shrimps are probably fairly abundant on the bank due to the overflow of warm water from the lagoon.

SNAPPING SHRIMP SPECTRUM CONTRASTED WITH WATER NOISE SPECTRUM

The main components of water noise occur in the frequency range 0–5 kc, as shown in Figure 10. The spectrum of water noise is shown by the dashed line in Figure 16, which represents an average of the intensity values at each 1-kc interval for each of the 17 stations where only water noise was heard. The graph shows that water noise decreases fairly regularly with increasing frequency. At frequencies above 8 kc the contribution of water noise to ambient noise is negligible.

Figure 11 is a vibrogram of shrimp noise west of Flatts Inlet, where water noise was at a minimum (sea state 1). The vibrogram is darkest in the frequency range 2–7 kc, indicating that shrimp noise is most intense in this range. Each spike, which represents an individual snap, exceeds the range of this vibrogram. In Bermuda, shrimp noise completely dominates water noise from 2 to 5 kc and to a lesser extent below and above this range (Fig. 16). Everest *et al.* (1948) and Knudsen *et al.* (1948) also found that above 2 kc shrimp crackle is the major source of ambient noise. Using a Pimanov analyzer, Shishkova (1958) found

that shrimp noise was greatest between 3 kc and 7.2 kc, but that the entire frequency spectrum of shrimp noise extends from 2.5 to 14 kc.

Unlike water noise, which decreases with regularity from 0 kc, there is a slight decrease of shrimp noise to 1 kc, then a slight increase to 2 kc, followed by a gradual decline with increasing frequency. This slight decrease of intensity at 1 kc appeared on many of the sections made (as in Figure 8) and is characteristic of snapping shrimp noise in Bermuda.

The average point of highest intensity of Bermuda shrimp noise is 2.2 kc, a point at which the relative intensity is 4.7. The point of highest intensity varied tremendously from station to station. Since shrimp noise level gradually decreases as the distance between bed and hydrophone increases (Everest *et al.*, 1948; Johnson, 1948), this variation in intensity was probably the result of differences in this distance.

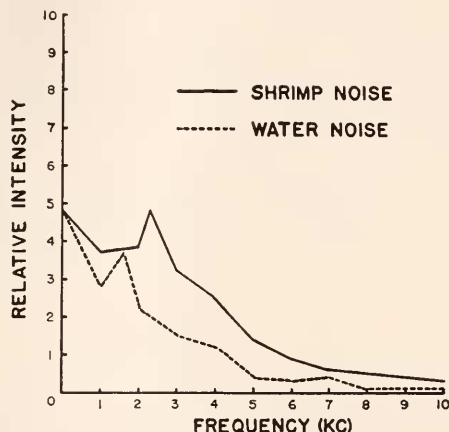


FIGURE 16. Spectra of shrimp and water noise at Bermuda.

The most reliable way to differentiate between the two types of noise is by noting the total frequency range. Snapping shrimp noise extends to frequencies of over 15 kc, but water noise is confined to the lower frequencies. Shrimp noise also differs from fish noise and spiny lobster stridulations, which are most intense at low frequencies (Loye and Proudfoot, 1946; Dobrin, 1947; Moulton, 1957).

VARIABILITY IN SHRIMP SPECTRA

A broad peak somewhere above 2 kc is characteristic of snapping shrimp spectra, but the frequency at which noise is most intense, as well as the degree of intensity, varies in different areas. Sound surveys in widely separated areas along the eastern and western coasts of the United States and in the Pacific Ocean have yielded a variety of shrimp noise spectra (Everest *et al.*, 1948). The point of highest intensity is different for each spectrum. Everest *et al.* found that in the San Diego Yacht Harbor, California, shrimp noise was most intense at about 2 kc, but in the Florida-Bahamas area it reached a peak at 10 kc. Analysis of shrimp noise in the Bimini area of the Bahamas, recorded during the summer of 1956 in

conjunction with a study of the acoustical behavior of some fishes in this area (Moulton, 1958), revealed that the shrimp noise is most intense in the frequency range 3–8 kc (Fig. 12). The main intensity band was about 1 kc higher than in the Bermudas (compare Figures 12 and 11).

Everest *et al.* attributed some of the differences among the spectra which they obtained to differences in the measuring equipment employed. However, it is probable that variability of shrimp spectra is an inherent one and not due entirely to the use of different equipment. One of our recorders was employed both in the Bermudas and in the Bimini area, yet different spectra resulted with the use of the same instrument. This 1-kc difference in the spectra is more likely due to differences in the genera and species of predominating shrimp inhabiting the two areas and, more important, differences in their habitats. In the Bermudas snapping shrimps preferably occupy rock crevices. This kind of habitat tends to produce an echo effect, which is reflected in an intense band at the lower frequencies. In the Bimini area, most of the species of snapping shrimp (predominately *Synalpheus* species) inhabit the channels and pores of enormous sponges. This tends to result in a higher-pitched crackle. Thus, the echo effect is greater in Bermudian waters and this is presumably what causes the band of greatest intensity to be 1 kc lower than at Bimini. This resonance effect was also present when snaps of animals in aquaria were recorded. A water-filled aquarium provides excellent conditions for the recurrence of echoes.

DIURNAL AND SEASONAL VARIATIONS

Studies by others demonstrated a diurnal variation in intensity of snapping shrimp noise, which increases slightly at night. Shrimp noise is 2 to 5 db higher at night than in the daytime, and it reaches a peak shortly after sunset and just before sunrise (Johnson *et al.*, 1947; Johnson, 1948). Knudsen *et al.* (1948) found that the peak in noise level is 3 to 4 db above the daytime level. A slight increase in activity of Bermuda populations during early evening was indicated (compare Stations 22 and 23). Animals other than snapping shrimp may indirectly cause an increase in noise level at this time by wandering about more then, thus inducing the shrimp to more snapping.

There is no significant seasonal variation in shrimp noise, at least in regions where the seasonal variation in temperature is small. Studies in the San Diego region, where water temperature remains relatively constant, showed no great fluctuations in noise level during the year (Johnson, 1948). Although no study of annual variations could be made in Bermuda, it is probable that in this region, as well as in all other areas where there is little seasonal variation in water temperature, there is little annual variation in shrimp noise. However, in places where there is a fairly large variation in water temperature, it is possible that temperature changes may have an effect on shrimp activity during the year.

CHARACTERISTICS OF SINGLE SNAPS

Individual snaps recorded in the laboratory were analyzed in order to compare them with the records obtained under natural conditions and to note any generic or specific differences in the spectra.

Individual snaps as they occur under the sea are essentially the same as those produced under laboratory conditions, but because of the great numbers of shrimp present, conditions under which the sounds are produced, and interfering water noise, differences in the spectra do exist. Where relatively few snapping shrimps occur and where water noise is at a minimum, the spectrum of a single snap is quite similar to that produced by an animal under laboratory conditions.

Recordings of *S. minus* snaps were made at the Bermuda Biological Station. The specimen was put in a wooden float (1×2 ft.) placed in sea water to a depth of 1 foot. A snap was recorded with the float 4 feet from the hydrophone (Fig. 13). Another snap was recorded when the float was 6 inches from the hydrophone, and still another with the specimen held in the hand 6 inches from the hydrophone. The spectra of these three snaps (Fig. 17) are almost identical. Thus, recording conditions do not significantly alter the spectrum of the snap. The main components of the *S. minus* snap lie in the frequency range 0–5 kc.

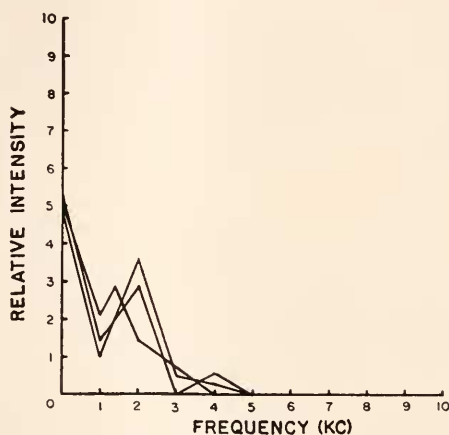


FIGURE 17. Spectra of three single *Synalpheus minus* snaps.

Synalpheus species are known to be prolific in the Bahamas and probably are the principal sound producers in this region. The laboratory records (Fig. 13) indicate that the point of highest intensity for *Synalpheus* lies in the range 1–2 kc, but the field records (Fig. 12) are most intense from 4 to 7 kc. When *Synalpheus* is not occupying a sponge pore, as in the laboratory recordings, its snap is most intense in the lower frequencies. But when, as in the waters of Bimini, it occupies its natural habitat within a sponge pore, the snapping noise becomes higher pitched, *i.e.*, its components are most intense at higher frequencies. This seems to indicate that variability in shrimp spectra around the world is to a greater extent the result of differences in habitat rather than differences in anatomy of the shrimp's claw.

Sounds produced by species of *Alpheus* were also recorded and analyzed. Figure 18 is a vibrogram and section of a single snap from *A. armatus* recorded at Bimini. This *A. armatus* snap is characterized by a narrow spike extending to

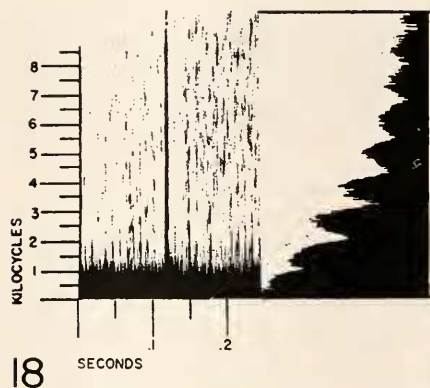


FIGURE 18. Vibrogram and section of a single *Alpheus armatus* snap.

FIGURE 19. Vibrogram and section of a single *Alpheus heterochelis* snap.

the higher frequencies. The section exhibits a "step-like" pattern. It is not known whether this pattern is peculiar to *A. armatus*; the recording is unique.

Single *A. heterochelis* snaps were recorded and analyzed at Bowdoin College. Two snaps from two different specimens, one rather large in size (4 cm. long) and a smaller one (2 cm. long), were recorded, one with a contact microphone and the other with a hydrophone. The specimens were placed in an aquarium with a total water volume of 89 cubic inches. The spectra of these snaps appear in Figure 20. There is some variation (probably due to the fact that sections cannot all be made at corresponding time instants with great precision), but varying size of specimen or type of recording microphone does not seem to alter the spectrum substantially.

Figure 19 is a vibrogram of an *A. heterochelis* snap in the 89-cubic inch aquarium, using a hydrophone. This snap is not in the form of a narrow spike as under natural conditions but covers a greater time interval, especially between

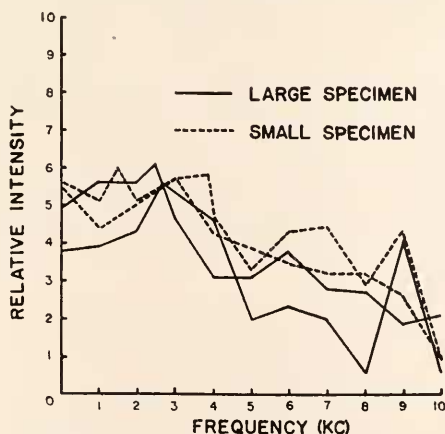


FIGURE 20. Spectra of four single *Alpheus heterochelis* snaps.

2 and 3 kc. This expansion is due to the echoes bouncing off sides of the aquarium and surface of the water. There is good evidence that snapping shrimp sounds are reflected from the water surface. Using a cathode-ray oscilloscope Everest *et al.* (1948) obtained oscillograms of individual snaps which show the sound wave itself and the echo, which is of smaller amplitude and opposite phase than the direct component. Because of echoing the sound seems to be much louder. This particular snap was easily heard by the unaided ear across the room.

It was found by increasing the frequency range to 704–70400 cycles per second that the *A. heterochelis* spectrum covered 52 kc. Johnson (1948) says that shrimp noise goes up to 50 kc. Shishkova (1958) analyzed the snaps of a snapping shrimp in a vessel and found the frequency band to be from 1 kc to only 6.3 kc. However, she does not mention the genus of the snapping shrimp nor does she describe the vessel. The low frequency range suggests the shrimp was a species of *Synalpheus*.

The spectrum of *A. heterochelis*, then, is quite different from that of *S. minus*. The *Alpheus* spectrum, which is greater than 10 kc., covers a much greater frequency range than the *Synalpheus* spectrum, which terminates at about 5 kc (compare Figures 17 and 20). Another noticeable difference is the amplitude of the peak intensity. In both cases the snap is most intense in the frequency range 1–4 kc, but the maximum intensity of the *Alpheus* snap is twice that of the *Synalpheus* one. Everest *et al.* (1948) noted some generic differences of wave shape between *Alpheus* and *Synalpheus* impulses. It seems clear that because claw structure of the two genera differ markedly, the sounds they produce would also be noticeably different. The structural pattern is uncertain. Whether dependable identifications can be made by sound analysis or not will be decided through further investigation.

SIGNIFICANCE OF SNAPPING SHRIMP NOISE

Shrimp crackle is useful as a tool in marine ecology. Information as to distribution of snapping shrimps can be obtained much more efficiently by this method than by laborious dredging, as Johnson (1948) pointed out. It is useful in determining depths and types of benthic environments. In the Bermuda area, at least, intense shrimp noise automatically indicates that the depth is less than 120 feet and that the bottom consists of coral, rocks, shells, or other sheltering materials. By spectral analysis it may be possible to pinpoint the type of substratum. Shrimp crackle may also be used indirectly to locate symbionts of the shrimp or other benthic animals inhabiting the same environment as the snapping shrimp. This use of shrimp noise has commercial implications. Detection of shrimp crackle with directional sound equipment may assist in finding commercial sponge concentrations, areas where the agar sea-weed *Gelidium* abounds, and fishing grounds (Johnson, 1948).

On the other hand, shrimp noise acts as a barrier in the study of underwater sounds. Because it is so intense and constant, it sets up a "curtain of sound" that makes it difficult to hear the sounds produced by other animals. Submariners are reputed to have masked engine and generator noise behind this acoustic curtain in wartime. But in any case, whether it is advantageous or not, it is there as the most persistent and most widespread biological noise.

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SUMMARY

1. The snapping mechanism of snapping shrimps of the genera *Alpheus* (*Crangon*) and *Synalpheus* has been studied and the "crackle" produced by populations of these shrimp surrounding the Bermuda Islands has been analyzed.

2. Differences in chela structure between the two genera are enumerated. Earlier beliefs that the sound is produced primarily by contact of the calcified tips upon closure of the dactylopodite on the propodite are corroborated. It is concluded that the "suckers" in the articulation of the joint in *Alpheus* species do not serve as a cocking mechanism, and it is suggested that suction develops in the living animal by depression of the membrane between the segments as the dactylus is raised. Overlapping exoskeletal knobs in the joint probably serve to hold the dactylus in place.

3. The structure and physiology of the chela musculature are as in the Crustacea generally. Both fast and slow contractions and an inhibitory effect are demonstrated. The functional significance of a doubly excitable system in this animal is discussed.

4. Analysis of snapping shrimp noise recordings at various locations around Bermuda shows that populations principally occur where sheltering materials are present and at depths of less than 120 feet. Prevailing temperature is also a limiting factor, since snapping shrimps occur mainly in tropical and subtropical waters.

5. In contrast to water noise, which is limited to the frequency range 0-5 kc, shrimp noise extends to frequencies of over 15 kc under natural conditions. Shrimp spectra from different areas are variable, due to differences in the predominating species inhabiting each area and, more important, to habitat differences.

6. There is a slight increase in shrimp noise at night but probably no significant seasonal variation at Bermuda, because water temperature remains relatively constant there throughout the year.

7. Under laboratory conditions generic differences in the spectra occur. The frequency range and amplitude of peak intensity of an *Alpheus* single snap are greater than in *Synalpheus*, as a result of the more powerful chela of *Alpheus*. Variation in recording conditions or size of specimen does not alter the spectrum substantially. The components of single snaps of specimens in aquaria extend to higher frequencies and cover a greater time interval than individual snaps under natural conditions because of greater echoing under laboratory conditions.

8. Snapping shrimp noise is useful in determining benthic environments and fauna.

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